Why is *Verbesina virginica* (Frostweed, Asteraceae) not found in grasslands?

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ABSTRACT

Factors determining a species ecological niche are difficult to identify. *Verbesina virginica* (Frostweed, Asteraceae) is widespread across eastern North America but not generally found in grasslands or savannas. It usually occurs under a canopy or at the edge of a canopy. In central Texas it is found below the canopy of *Quercus virginiana* (live oak), *Ulmus crassifolia* (cedar elm) and a few other species. In order to better comprehend conditions limiting its distribution and niche requirements, a factorial experiment was performed. Three factors were examined including canopy (+ or -), additional water (+ or -) and neighbors (+ or -). Response variables were mortality, stem diameter, plant height, number of leaves, area of the largest leaf and aboveground dry mass. Total plant survival at the end of the experiment (234 days) was 28% or 27/96 plants. Survival was greatest below the canopy at 48% (23/48), while in the open it was 8% (4/48). Survival was greatest below the canopy in the no water, no neighbors treatment at 83%, but with no neighbors and additional water it was 50%. In the no canopy treatment, survival was 0% with the no water, no neighbors treatment and 11% with water, but no neighbors. Aboveground dry mass produced below the canopy was 64.7 g with a mean of 2.9±1.5 g/plant. Aboveground dry mass in the open was 9.1 g with a mean of 2.3±1.0 g/plant. Survival and dry mass was greatest for plants below the canopy, with no supplemental water and no neighbors. Survival was lowest when neighbors were present in the open or below the canopy and with or without supplemental watering. *Verbesina virginica* is mostly found in canopy shade because of the lack of C4 grasses and other herbaceous plants that probably take up water more efficiently during the hot-dry time of year. Thus, it is not found in canopy gaps because of the growth, competition and probably water uptake and use by the high temperature tolerant C4 grasses. Published on-line www.phytologia.org *Phytologia 98(1): 76-88 (Jan 5, 2016)*. ISSN 030319430.

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When a species is found in a given location, it is because that species can tolerate or requires the conditions present in that area. It is difficult to determine a species niche requirements, but more difficult to decide why it is not found in another place with similar conditions. Measuring density of terrestrial plants is relatively easy to do (Van Auken et al. 2005), but sorting out the factors that govern why a species is present where it is found is much more challenging (Begon et al. 2006). Some species are found in specific communities or at the edge of a community, whereas others are not constrained. Species may be limited spatially or temporally by abiotic or biotic factors or combinations (Begon et al. 2006; Leonard and Van Auken 2013; Louda and Rodman 1996; Maron and Crone 2006; Valladares and Niinemets 2008), but limiting factors may not be easily visualized.

Verbesina virginica seems restricted to growing below a canopy in shade (Gagliardi and Van Auken 2010). However, high carbon uptake in high light suggests *V. virginica* should be able to grow in high light, non-shaded open areas. When open grasslands, savannas or gaps were examined, *V. virginica* was not present. Similar situations have been reported for other species. For example, *Strepthanthus bracteatus*, a rare mustard found only in central Texas, occurred below a *Quercus verginiana/Juniperus ashei* (live oak, Fagaceae/ashe juniper, Cupressaceae) canopy unless the plant was protected from herbivory (Leonard and Van Auken 2013). Another mustard (*Cardamine cordifolia*, bittercress) was restricted to shaded habitats because of chronic insect herbivory in full sun (Louda and Rodman 1996). Many studies have indicated herbivory can have major effects on plant abundance, dynamics, distribution and community composition (see Maron and Crone 2006).Woody plants have long been restricted from most grasslands because of high fire frequency (see Collins and Wallace 1990; Van Auken 2000), but with the introduction of large numbers of domestic herbivores, fuel mass has decreased as has fire frequency, with a concomitant increase of woody plants in grasslands (Van Auken 2000, 2009).
Unfortunately, the reason that *V. virginica* is not present in grasslands is undefined.

In central Texas, savannas are associated with grasslands, woodlands or forests (Van Auken and McKinley 2008; Van Auken and Smeins 2008). A species found in some of these woodland communities or edge communities is *V. virginica* L. (Frostweed, Asteraceae) (Correll and Johnston 1979; Strother 2006). It appears to be an understory species, sometimes forming almost mono-specific communities (Gagliardi and Van Auken 2010). It can establish below some species, but no studies were identified concerning which species, its light requirements, essentials for establishment or successional status (Enquist 1987).

Light level is an important factor limiting or controlling the presence of many species in various communities (Begon et al. 2006; Smith and Smith 2012). Species growing in shady habitats have reduced photosynthetic rates, lower light saturation, light compensation points and dark respiration compared to those growing in full sun (Boardman 1977; Begon et al. 2006; Larcher 2003; Valladares and Niinemets 2008). Adaptive crossover is displayed by some species allowing them to acclimate to high or low light environments and have a broader ecological niche (Givnish et al. 2004).

Verbesina virginica had a fairly high photosynthetic rate which was surprising for a species found in shade below a canopy (Gagliardi and Van Auken 2010). A related species, *V. encelioides*, had an A_{max} of 12.3 µmol $CO_2/m^2/s$, which is within the range reported for *V. virginica*, but *V. encelioides* is a disturbance species and not expected to do well at low light levels below a canopy (Gleason et al. 2007). Another species, *V. arborea*, a tropical species, grew well in open grazed plots where seed was added, suggesting it was a sun species as well (Posada et al. 2000). Our conundrum was why did *V. virginica* have an unusually high photosynthetic rate and grow in low light below a canopy, but not in adjacent grasslands?

PURPOSE

Our hypothesis was that *V. virginica* did not compete well with associated herbaceous species and consequently was forced into a secondary habitat where it survived and grew quite well because the C_4 grasses were not present and the shade adapted C_3 species were limited.

METHODS

This study was carried out in the City owned Phil Hardberger Park in San Antonio, Texas, USA

(N-$29^{o}33$"41.3", W-$98^{o}31$'11.8"). Most of the subsurface of the area is Cretaceous limestone, and soils are usually shallow, rocky or gravelly, dark colored, calcareous with neutral or slightly basic pH, usually Austin silty clays, Whitewright-Austin complex, or Eckrant cobbly clay (Taylor et al. 1962; NRCS 2006).

The area is approximately 20 km south of the Edwards Plateau region of central Texas just south of the Balcones Escarpment in northern Bexar County (Correll and Johnston 1979; Van Auken et al. 1981; Van Auken and McKinley 2008). The elevation of the study area is approximately 350 m above mean sea level (AMSL) (Taylor et al. 1962; NRCS 2006). Mean annual temperature is approximately 20.0°C with monthly means from 9.6°C in January to 29.4°C in July (NOAA 2004). Precipitation is 78.7 cm/yr, bimodal, with peaks in May and September (10.7 cm and 8.7 cm), little summer rainfall, high evaporation and high variability (Thornthwaite 1931; NOAA 2004).

Verbesina virginica L. (Frostweed, Asteraceae) can be up to 1.8 m tall, and is an erect, unbranched, herbaceous, perennial plant with the main stem prominently winged (Figure 1A and B). It is frequently found in the eastern United States and its western limit of distribution is Kansas, Oklahoma and Texas (Correll and Johnston 1979; USDA 2009). In central Texas, it is mostly found beneath the canopy of *Quercus virginiana* (live oak, Figure 1C), Q. *stellata* (post oak), Q. buckleyi (Texas red oak), *Ulmus crassifolia* (cedar elm) and *Juniperus ashei* (ash juniper), usually on deeper soils in some of these communities (Gagliardi and Van Auken 2010). Its common name comes from ice crystals that surround the stem usually after the first freeze (Figure 1D).

Verbesina virginica can form mono-specific communities in understory habitats especially on deeper soils including some riparian soils. Isolated plants are occasionally found below the canopy in some upland central Texas communities (Enquist 1987). Leaves are large and ovate to oblong-lanceolate and pubescent. Flowering is in late summer concluding with cold temperatures and frosts in late fall. The flower heads usually have three to four white to greenish white ray flowers and up to 15 disk flowers. It tolerates high temperatures but leaves are usually wilted during dry conditions. The rooting system is unreported but is probably a deep tap root and we do not think the plants are connected via rhizomes.

Area vegetation in this region was savanna or woodland with *Juniperus-Quercus* (juniper and oak) communities being dominant, but higher in woody plant density than communities farther to the west (Smeins and Merrill 1988; Van Auken et al. 1981; Van Auken and McKinley 2008.). High density woody species are *Juniperus ashei* (Ashe juniper) and *Quercus virginiana* (=*Q. fusiformis*, Live oak) followed by *Diospyros texana* (Texas persimmon) and *Sophora secundiflora* (Texas mountain laurel). *Ulmus crassifolia* (cedar elm) is found in these communities, but usually at lower density and on the deeper soils. There are also former grasslands of various sizes that are woodlands today with *Prosopis glandulosa* (mesquite), *Aloysia gratissima* (whitebrush) and *Diospyros texana* as major woody species. These areas seem to be on deeper soils and were not used in the current study. Within the *Juniperus- Quercus* woodlands there are sparsely vegetated intercanopy patches or gaps on shallow soil (openings in the woodlands) (Van Auken 2000). This is where the high light or open treatments were placed.

The most important herbaceous species below the canopy are *Carex planostachys* (Cedar sedge) (Wayne and Van Auken 2008) and *V. virginica* (Gagliardi and Van Auken 2010). In the gaps, *Aristida longiseta* (Red three-awn), *Bouteloua curtipendula* (Side-oats grama), *Bothriochloa* (=*Andropogon*) *laguroides* (Silver bluestem), *B. ischaemum* (KR bluestem), various other C4 grasses, and a variety of herbaceous annuals are common (Van Auken 2000).

Experimentally, a three factor, factorial experiment was set up. The factors were canopy or no canopy (+ or - canopy), added water or no added water (+ or - water), and neighbors or no neighbors (+ or - neighbors). There were two physical locations, two levels of added water and neighbors were present or removed. The experiment included 12 replications for each treatment.

Plants were started from seed and grown for 60 days in 10.1 x 10.1 cm peat pots (in a greenhouse) in native area soil from the study site (dried, sifted Whitewright-Austin complex) with 100 ml of a complete nutrient solution added initially (Van Auken, et al. 2005). There were 12 replications of each treatment for a total of 96 pots or plants (2 positions, 2 water treatments, 2 neighbor treatments, and 12 replications or 2x2x2x12=96 total pots or plants). Plants were randomized and planted in the field March 7, 2013. All plants were watered initially and then every other day with 500 ml of tap water for two weeks. After that, only the water + treatment plants were given tap water and only once/week.
Watering was done to maintain the soil at approximately field capacity. Basal diameter, height and number of leaves as well as the size of the largest leaf was measured monthly. Stem and leaf area were calculated. Live and dead plants were counted monthly. Upon harvesting, when growth had stopped (day 234), shoots were clipped at the soil surface and dried at 75°C to a constant level and then mass was determined. Roots were not collected. Light levels were measured at each plant position using a LI-COR® LI-190 SA integrating quantum sensor. A total of 96 measurements were made, and values were averaged for each position (Van Auken 2000).

Analysis of variance was used for final results (Sall et al. 2001). This was used to test the effect of canopy position, added water and the presence of neighbors on response variables. Interactions that were not significant were removed from the models. Least square regressions were completed to examine how mortality and other response variables changed in time. Data were compared to various functions. Significance level for all tests was 0.05.

RESULTS

The experiment was planted on March 7, 2013 and harvested 234 d later on November 1, 2013. Overall mortality, at the end of the experiment, was 72% or 69/96 dead and survival was 28% with 27/96 total plants surviving. Mortality of *Verbesina virginica* increased through the experiment (Figure 2) and was greatest in the open or full-sun at 92% (44/48) with four survivors. Below the canopy in shade, mortality was 52% (25/48) with 23 of 48 plants surviving or 48% survival. Mortality was a significant linear function (Figure 2) and transformations did not significantly increase the coefficient of determination (R^2) or P value (not presented). Time (days) explained 90-95% of the variation of total and below canopy mortality of *V. virginica* (*Figure 2*).

Four plant growth factors were measured during the experiment including plant height, number of leaves, length and width of the largest leaf and basal stem diameter. Largest leaf area was calculated as was stem basal area. These factors were regressed on time in days that they were measured or counted. Linear as well as logarithmic and polynomial (2nd, 3rd and 4th order) regressions were examined. None of the linear and logarithmic regressions were significant ($P>0.05$ in all cases).

Height for all living plants was significant as a 2nd degree polynomial (Figure 3). The R^2 for all plants was 0.58. For plants growing below the canopy it was 0.66 and for plants grown in the open (no canopy) it was 0.47. Thus, the R^2 for a 2nd degree polynomial function explained 47-66% of the variation in height of *V. virginica* over the time in days of the experiment (Figure 3).

The number of leaves, leaf area and mean basal stem diameter were all significantly related to time but were 2nd, 3rd or 4th order polynomial functions. These polynomial regressions explained 57-86% of the variation of that factor in time. All measured factors increased from the start of the experiment in March of 2013 through the spring months and reached a peak in late June (on day 107) and then declined through late summer and fall until the experiment was terminated and plants were harvested in November (on day 234). *Verbesina virginica* plants were largest on the 107th day of the experiment (Table 1), with plants in the open (no canopy) being the tallest, had the greatest number of leaves and stem basal diameter, but leaf area of the largest leaf was the same for plants from both positions, but differences were not significant.

Table 1. Mean height, number of leaves, area of the largest leaf and stem basal diameter of *Verbesina virginica* plants on June 27, 2013 the 107th day of the experiment when plants were largest.

	POSITION	
RESPONSE VARIABLE	CANOPY	NO CANOPY
HEIGHT (cm.)	12.7	15.5
NUMBER OF LEAVES	8.0	10.3
AREA-LARGEST LEAF (cm^2)	44.2	44.3
STEM BASAL DIAMETER (mm.)	2.66	3.25

Considering final plant dry mass, canopy position was a significant main effect in the experiment, while added water or the removal of neighbors were not significant (Table 2). The total number of live plants at the end of the experiment below the canopy and in the open (no canopy) are shown in Figure 4A. The largest number of live plants was below the canopy and that is where the greatest dry mass was produced (Figure 4B). However, there was a significant position (+ or - canopy) x neighbor (+ or -) interaction (Table 2, Figure 5A). If plants were in the open (- canopy), with or without neighbors, dry mass was less than one gram per plant. If plants were below the canopy with neighbors, dry mass was about 2 grams per plant, but with neighbors removed, dry mass was 3.45 g/plant. Survival of *V. virginica* plants with neighbors and no canopy was three plants (Figure 5B), but was one plant if neighbors were removed. Below the canopy with neighbors, survival was nine plants, but if neighbors were removed, survival was 13 plants.

In the bar graph showing all of the treatments, dry mass was greatest in the two canopy treatments without neighbors (Figure 6A). Dry mass was highest in the +canopy treatments and lowest in the – canopy treatments. The number of live plants was greatest in the + canopy treatment and lowest in the – canopy treatments (Figure 6B).

Table 2. ANOVA table with results comparing *Verbesina virginica* plant dry mass with canopy position (canopy no canopy), water (added water or none added), neighbors (present or removed) and their interactions are included. *F*-ratio and *P* values are presented in the table with significant *P*-values in bold and *.

Source	*F*-Ratio	*P*-value
Canopy (C)	19.2710	**<0.0001***
Water (W)	0.0091	0.9224
Neighbors (N)	2.0386	0.1568
C x W	0.2322	0.6311
C x N	4.9024	**0.0294***
W x N	1.2795	0.2611
C x W x N	1.2297	0.2705

When the sum of the final aboveground dry mass was examined, there was seven times as much dry mass below the canopy (64.7 g + canopy or in the shade) compared to the – canopy or open, full sun treatment with only 9.1 g. The mean above-ground plant dry mass below the canopy was 2.9±1.5 g/plant and mean above-ground plant dry mass in the open was 2.3±1.0 g/plant. Dry mass was greatest for plants below the canopy, with no neighbors (Figure 6A and B). Survival was lowest when neighbors were present in the open or below the canopy and without supplemental watering. The sum of the dry mass when neighbors were removed was twice as high below the canopy compared to when neighbors were not removed (Figure 7).

Verbesina virginica survival was greatest in canopy shade where soil was approximately 50% deeper (Table 3) and light levels were 5.7% of light levels in the open position (–canopy).

Table 3. Comparison of light levels and soil depth for *Verbesina virginica* with an *F*-test with canopy position (canopy no canopy) as the main treatment. Means, standard deviations, *P*-values and percent of no-canopy values are presented in the table with significant *P*-values in bold and *.

	CANOPY	%	NO CANOPY	*P*-VALUE
LIGHT LEVEL(μmoles/m^2/s	108±125	5.7	1905±303	**<0.0001***
SOIL DEPTH (cm.)	13.48±6.80	150.7	8.94±4.49	**<0.0053***

DISCUSSION

During this and previous studies, *Verbesina virginica* was found below or at the edge of the canopy of *Q. virginiana* or *U. crassifolia* (Figure 1), but not in associated grasslands. Planting *V. virginica* in the open (no canopy) resulted in high mortality (Figure 2). No *V. virginica* plants were seen in the grassland during this study or in a previous study (Gagliardi and Van Auken 2009), but reports from the literature are not consistent concerning where it is found (Enquist 1987; Strother 2006; USDA 2009).

Light levels appeared to be important, with almost no *V. virginica* plants found in the high light open grassland habitat and few survived if they were planted there (Figure 4). Additionally, grassland soil was not as deep as the soil below the canopy (Table 3). Furthermore, *V. virginica* was not expected in the more shallow soils of the arid upland communities (Van Auken et al. 1981).

The presence of neighbors was also important and possibly the most important factor in determining the presence of *V. virginica*, but it was not a significant main effect in the current experiment (Table 2). Thus, the presence of neighbors seem to be a more subtle but not less important factor in influencing or determining the presence, density and the distribution of *V. virginica* in these communities. Neighbor effects seemed to be combined with one or more other factors, thus an interaction. The various C4 grasses in the open and the C3 sedge, *Carex planostachys* below the canopy may be more efficient in taking up water and possibly nutrients and thus reduce the possibility of *V. virginica* easily establishing in these habitats (Wayne and Van Auken 2009). The inhibiting effects of the C4 grasses seems to be paramount, but may be transitory and the high mortality of all *V. virginica* plants in the grassland habitat prevented us from teasing apart the potential neighbor and water effects in the current experiment (Figure 4). We don't know how long understory *V. virginica* plants would persist if the canopy were removed.

Finding positive and negative interactions between species is not unusual (Harper 1977; Grace and Tilman 1990, Fargione and Tilman 2005, Elliott and Van Auken 2014), but demonstrating the potential cause of the effect is much more difficult to do (Louda and Rodman 1990; Begon et al. 2006; Marion and Crone 2006; Valladares and Niinemets 2008; Smith and Smith 2012; Leonard and Van Auken 2013). Usually multiple abiotic factors interact to control the kinds of plants present in a given habitat.

However, it is the species response to these abiotic factors and their biotic interactions with them that will determine the community composition. These factors are dynamic and individuals are responding to them all of the time which makes it difficult to know which one or ones are controlling their responses and thus community composition. Because a species is present in a community does not mean it was there yesterday or will be there tomorrow.

Light levels and a species response to them are easy to understand singly, but when a species responds to other factors and other species at the same time, understanding or disentangling which factors are most important, if any, is difficult. Shade leaves of *V. virginica* plants in the low light environments of canopy trees, were capable of a high maximum photosynthetic rates (A_{max}), which is not typical of species growing below a canopy (Begon et al. 2006). Shade adapted leaves of various eastern deciduous forest understory species usually had A_{max} values lower than those reported for *V. virginica* (Hull 2002; Gagliardi and Van Auken 2010). Other photosynthetic parameters reported for *V. virginica* were in the range expected for shade adapted plants not sun species (Valladares and Niinemets 2008), but they were measurements of shade, not sun leaves.

Verbesina virginica has a fairly broad distribution, especially in the eastern United States. But very little is reported about its growth responses to light levels or other environmental factors. Most of the parameters measured for shade leaves suggest that this species is a shade adapted species, but A_{max} rates do not agree suggesting it can grow in full sun where we didn't find it and almost all of the plants placed or grown in full sun or open habitats died. Usually, true understory species have much lower photosynthetic rates than the rates previously reported for *V. virginica*. For example, *Carex planostachys* from the central Texas Edwards Plateau *Juniperus* woodland understory had an A_{max} value of 4.9 ± 0.3 $\mu molCO_2/m^2/s$ which was lower than the A_{max} for shade leaves of *V. virginica* and reached light saturation at low light levels (Wayne and Van Auken 2009). While *V. virginica* in central Texas is typically found growing in shaded habitats or the edge of woodlands, its high A_{max} for shade adapted leaves compared to other herbaceous shade plants would suggest it could grow in a variety of light environments including open habitats, but it was not found there.

Some plants can occur in a variety of light environments including some plants from disturbed (open) communities growing in shade (Bazzaz and Carlson 1982). Plants like *V. virginica* that have a relatively high A_{max} that changes little over a wide range of light levels could do well in shade with the presence of sunflecks (Hull 2002). However, there is nothing in the literature about *V. virginica* and its ability to grow in variable light. Stomatal conductance and transpiration reported for *V. virginica* previously were similar to a number of other species, but not compared with the native C_4 grasses (Gagliardi and Van Auken 2010). Xylem water potential of this species has not been measured or compared. Water use efficiency of this species should be examined closely with and without C_4 neighbors and at high and low light levels (Larcher 2003; Grunstra and Van Auken 2015). Results of studies like this would help determine why *V. virginica* is not found in open grasslands.

Verbesina virginica showed interesting photosynthetic responses in previous studies (Gagliardi and Van Auken 2010). These physiological responses to various light levels more than likely are contributors to the apparent niche observed for this species in the field. In general, resource utilization is spatially partitioned among species along environmental gradients, such as changes in light from open areas to woodland or forest edges (Wayne and Van Auken 2009; Gagliardi and Van Auken 2010). The ability of *V. virginica* to reach high photosynthetic rates at lower light level, its light saturation, and light compensation point allow it to exist in shaded environments. At light levels below 300 $\mu mol/m^2/s$, data suggests that other more shade tolerant species such as *C. planostachys* would probably be able to out-compete *V. virginica* (Wayne and Van Auken 2009), but not after *V. virginica* was established because of the deep shade below its canopy. At light levels above 300 µmol/m^2/s below the canopy, *V. virginica* could dominate, in part because it has photosynthetic rates as high as or higher than most co-occurring species and its large leaves would reduce light levels to very low values below its canopy (Grunstra 2008; Furuya and Van Auken 2009; Wayne and Van Auken 2009). However, its absence in associated grasslands is not explained. The established C4 grasses would have equal or higher photosynthetic rates, have higher water use efficiency and perhaps be more tolerant of higher light levels and lower soil water levels than *V. virginica.*

CONCLUSIONS

Frostweed survival was low in open areas without a canopy and highest in canopy shade. Below the canopy, removal of neighbors is important and suggests it is not a good competitor. It can establish and grow in full sun or open areas but seems to require a disturbance to do so. In addition there would have to be seeds present in the soil in order for it to take advantage of the disturbance, especially if the disturbance was small.

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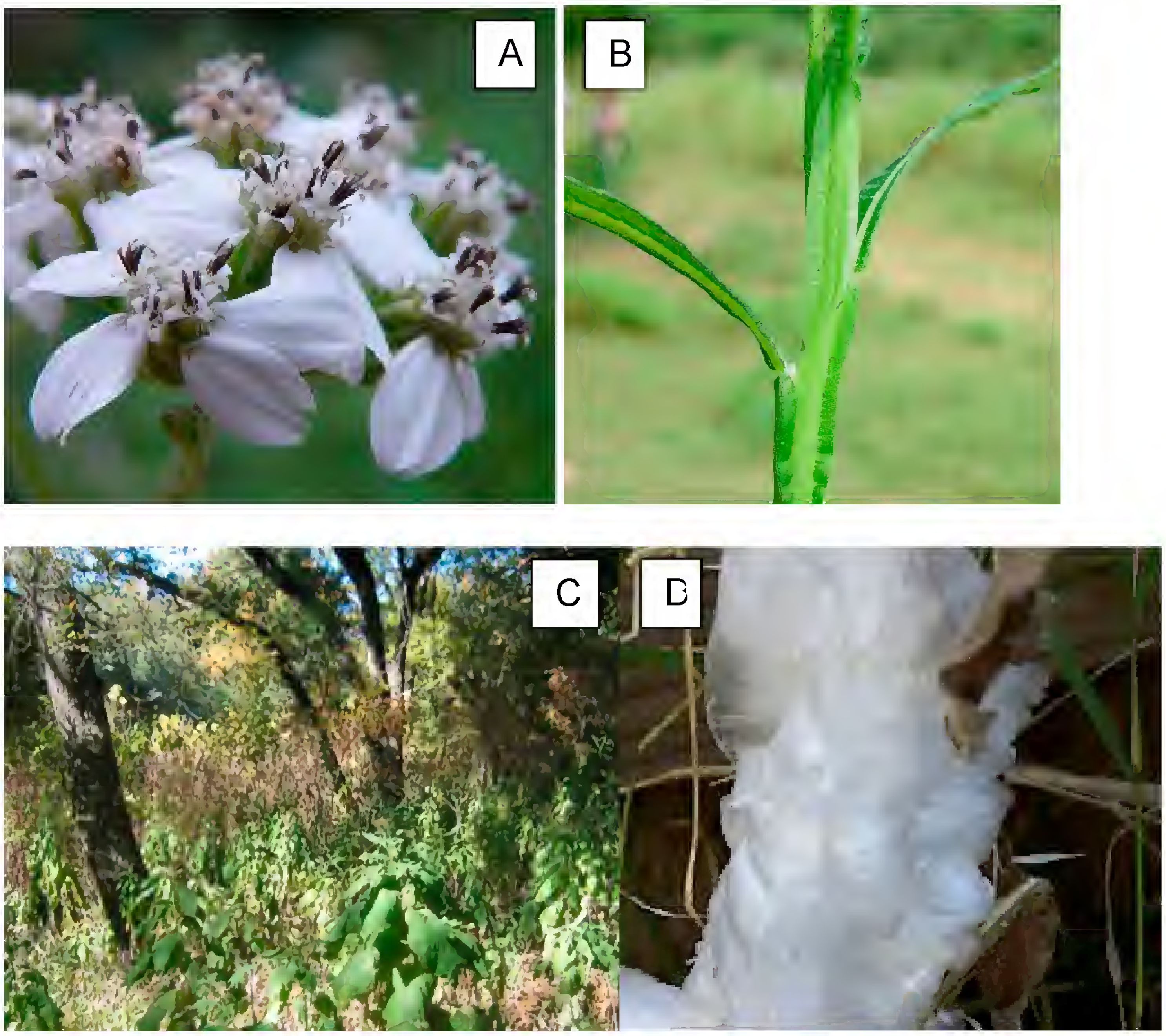


Figure 1. Photographs of some *Verbesina virginica* plant characteristics. Floral characteristics are shown in (A) and flower heads have both disk and ray flowers. The wings that are present on the stem are shown in (B). A habitat photograph (C) shows *V. virginica* below the canopy of several live oak trees (*Quercus verginia*). The characteristic ice around the stem of *V. virginica* after a frost or freezing temperature is also shown (D). Photos were taken by J. Gagliardia.

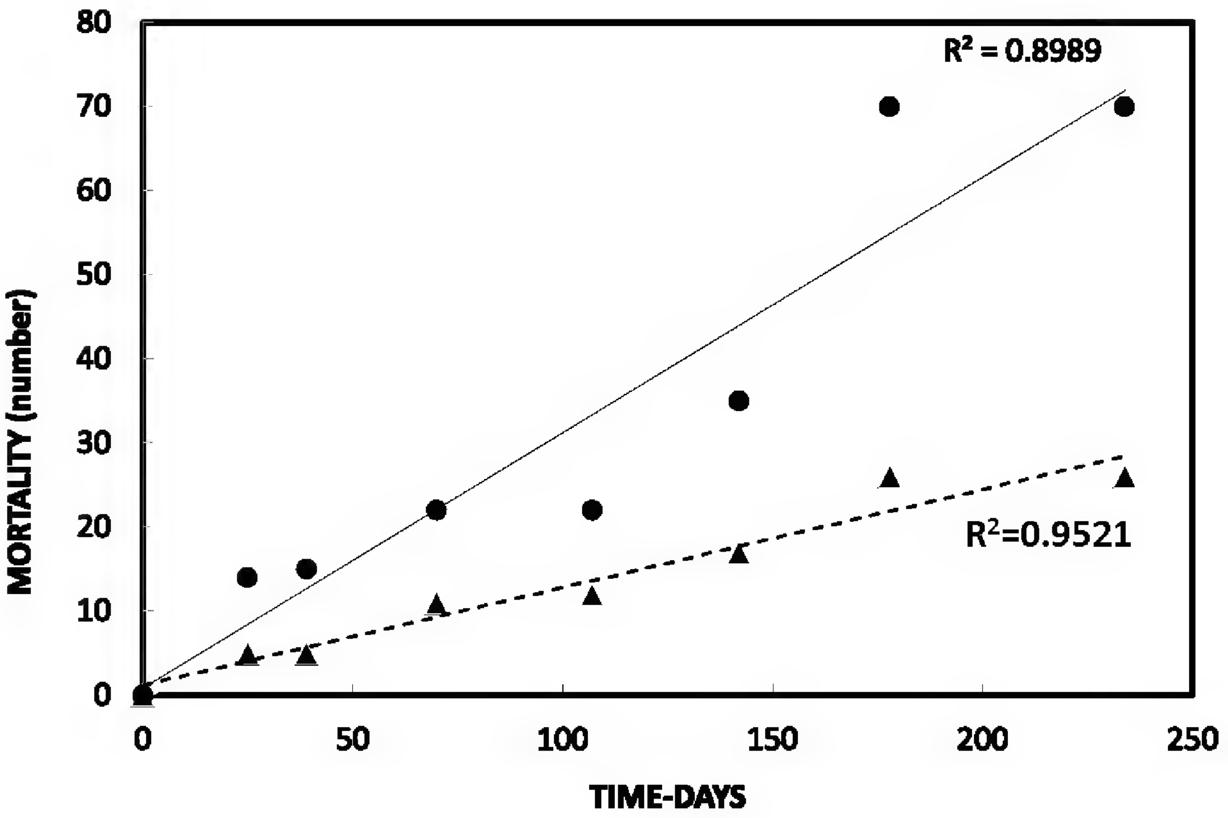


Figure 2. Mortality of *Verbesina virginica* plants at Hardberger City Park in San Antonio, Texas, USA (N-29°33"41.3", W-98°31'11.8"). Mortality of 96 plants (48 plants below a canopy and 48 plants in the open) were followed for 234 days in 2013. Total mortality is displayed (●) solid line and is a linear function ($y=0.3036x + 0.8313$, $P < 0.001$) as is mortality below the canopy (▲) with a dashed line ($y=0.1164x + 1.1867$, $P < 0.001$). Mortality was greatest in the open and increased to 92% or 44 out of 48 plants at the end of the experiment and is a linear function ($y=0.1881x + 0.3223$, $P < 0.01$) but is not shown.

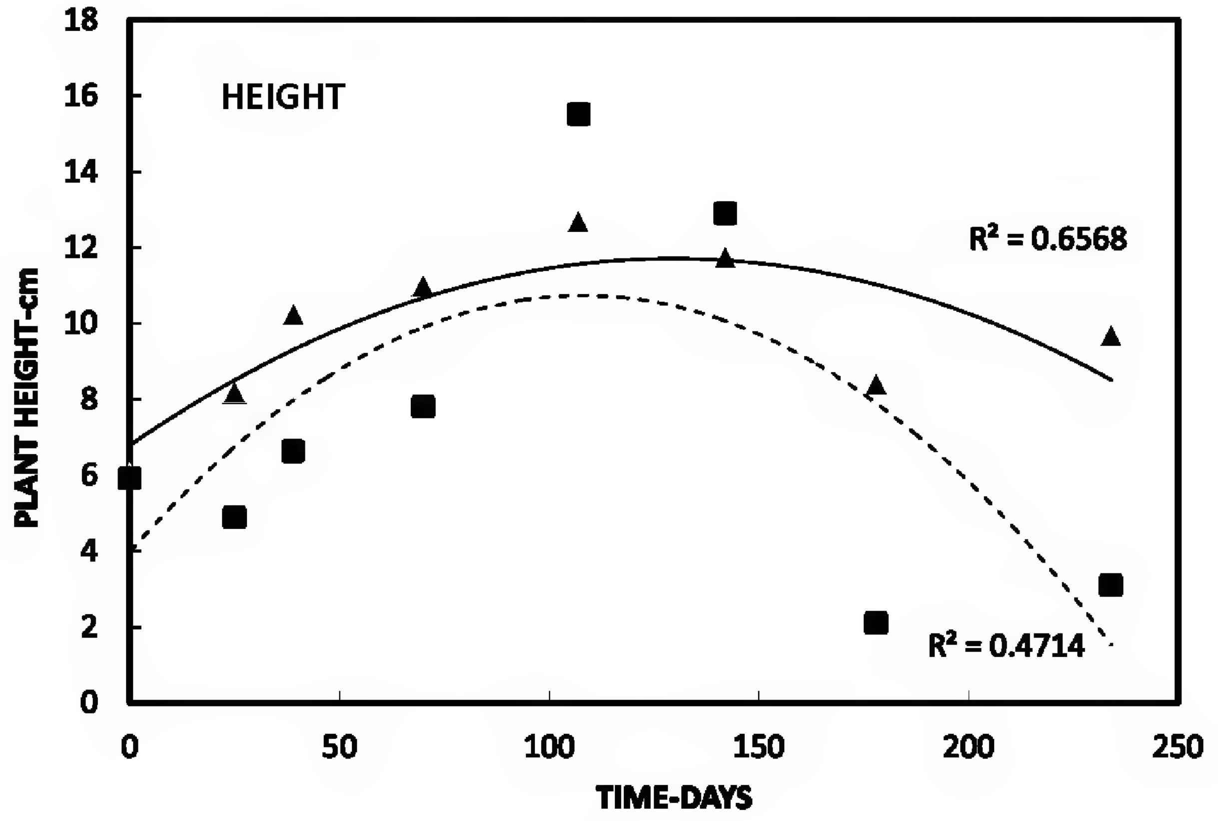


Figure 3. Height of *Verbesina virginica* plants at Hardberger City Park in San Antonio, Texas, USA. Height of plants was measured in centimeters approximately once per month over the course of the experiment. Lines are 2nd order polynomial functions and coefficients of determination (R^2) are presented. The triangles (▲) are for the plants below the canopy ($y = -\ 0.0006x^2 + 0.1251x + 3.97$, $P < 0.05$) and the squares (■) and dashed line are for open grown plants (no canopy, $y = -0.0003x^2 + 0.076x + 6.78$, $P < 0.05$).

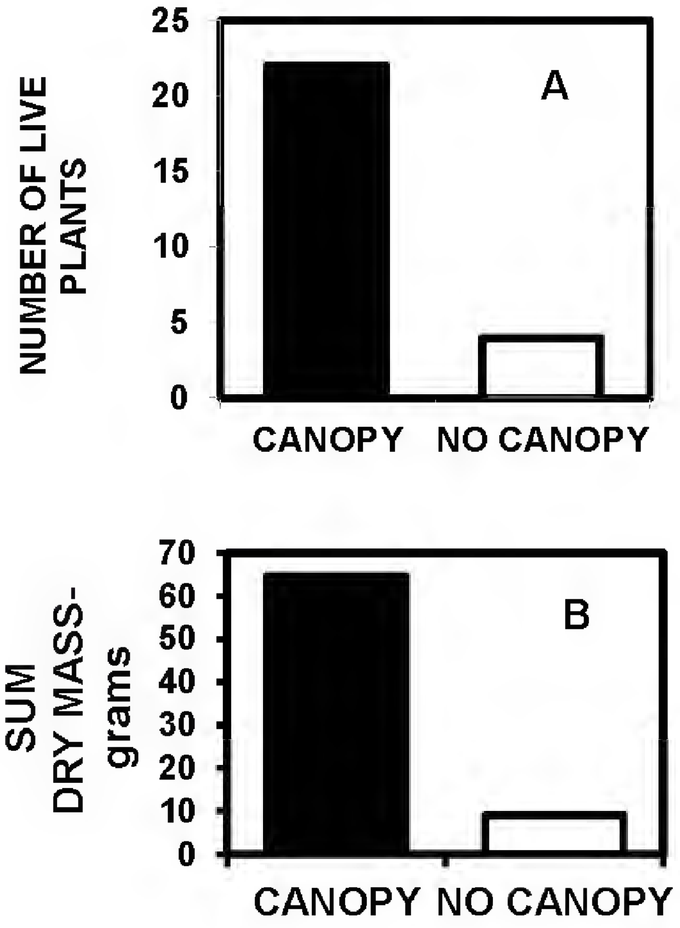


Figure 4. Number of live plants (A) at the end of the experiment below the canopy and in the open (No Canopy). Sum of live plant dry mass in grams (B) at the end of the experiment below the canopy and in the open (No Canopy)

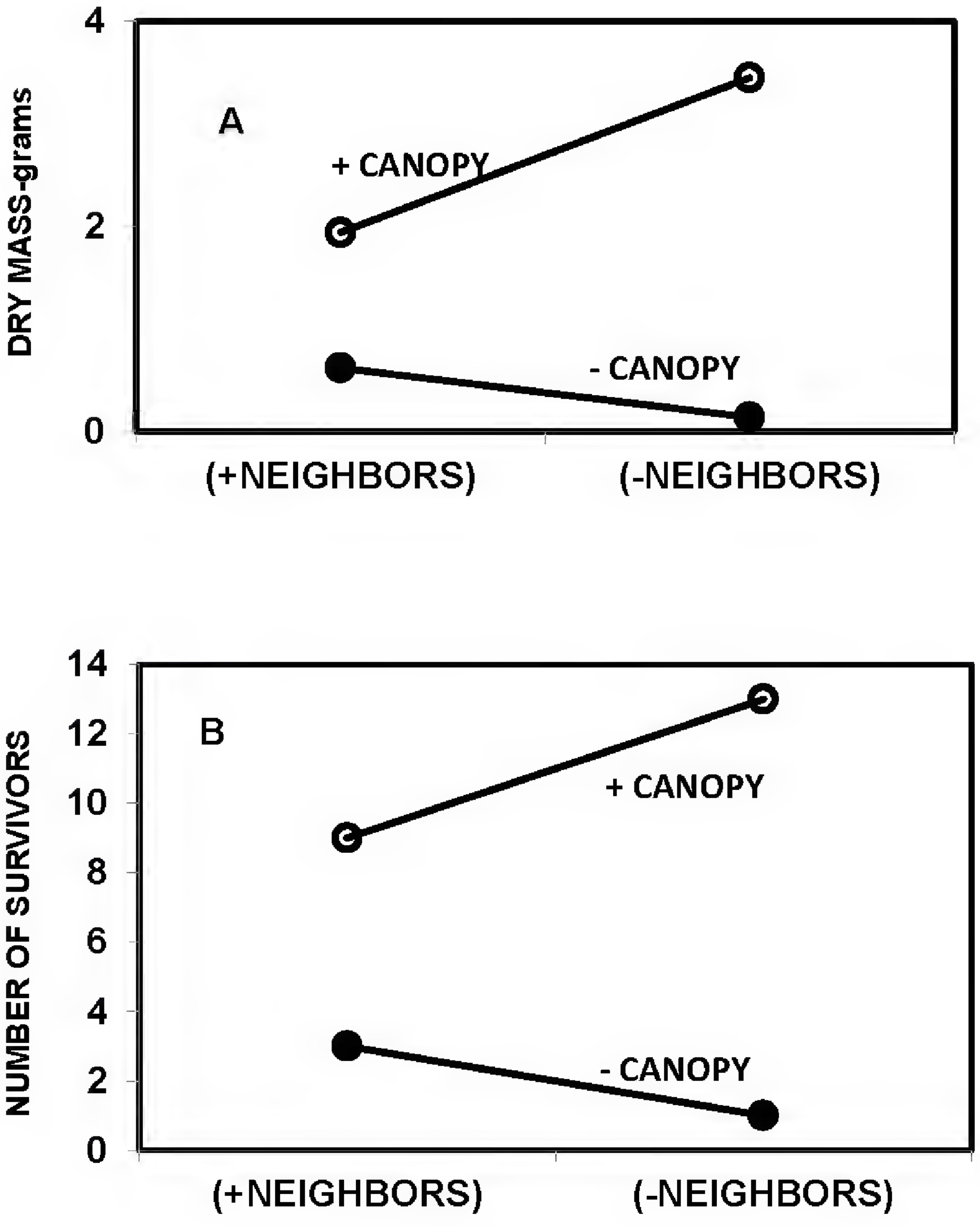
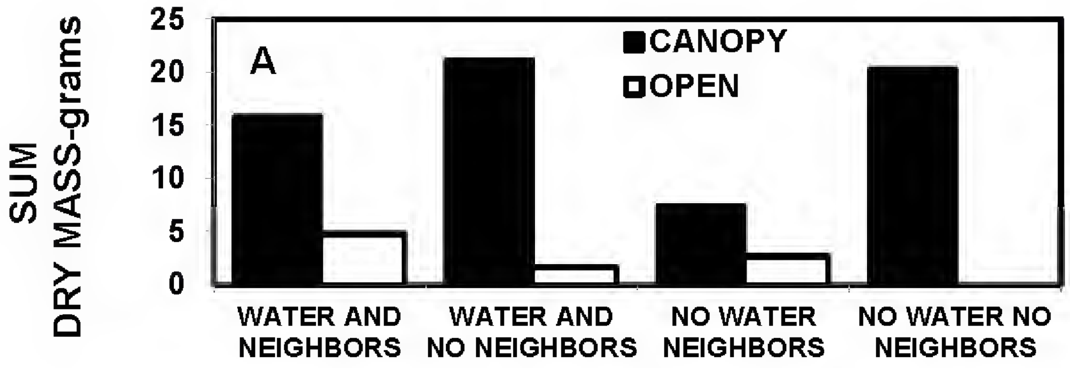


Figure 5. Interaction plot (A) of *Verbesina virginica* plant dry mass in grams with position +canopy or – canopy and + or – neighbors and (B) the number of survivors. Significant two way ANOVA interaction for (A) position and neighbors with F = 4.9024 and P = 0.0294 but (B) was not significant.



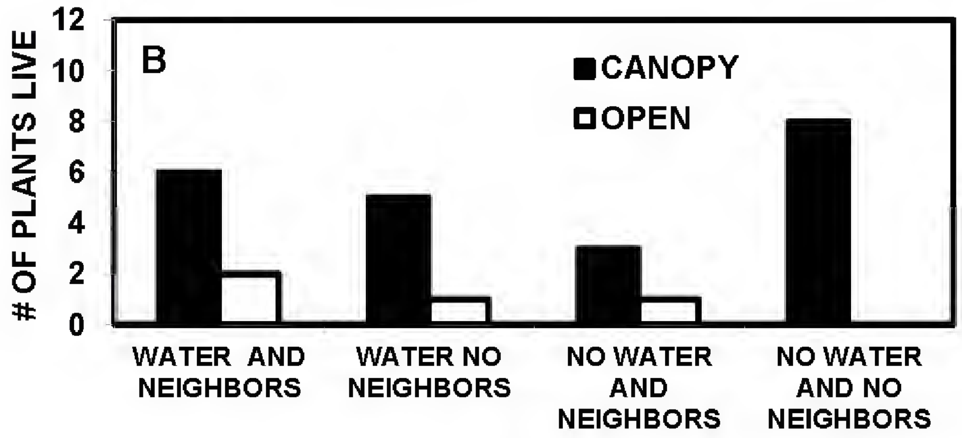


Figure 6. Sum of dry mass in grams (A) was greatest in the canopy treatment (black bars). Greatest dry mass was in the canopy and no neighbor's treatment with or with no added water. Total survival (B) was greatest in the canopy treatment (black bars) at 48% or 23/48. Greatest survival was in the canopy no water and no neighbor's treatment at 75% (9/12) and there were no survivors in the open in this treatment.

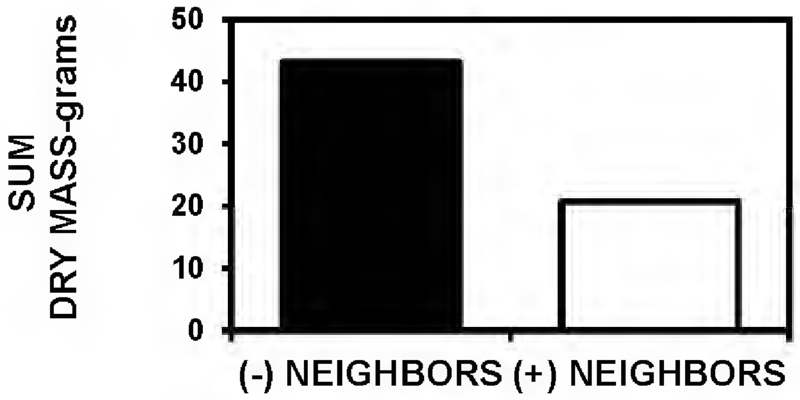


Figure 7. Sum of dry mass in grams produced by + canopy grown *Verbesina virginica* with no neighbors or with neighbors.